OSTEOLOGICAL DEVELOPMENT OF THE ANTARCTIC SILVERFISH *PLEURAGRAMMA ANTARCTICUM* (NOTOTHENIIDAE)

by

O.S. VOSKOBOINIKOVA (1), O.YU TERESHCHUK (2) and A. KELLERMANN (3)

ABSTRACT. - The paper presents a study of the osteological development of the Antarctic silverfish *Pleuragramma antarcticum* Boulenger (Nototheniidae). In comparison with other investigated nototheniids the development and ossification of the basioccipital and exoccipital were found to occur late in the neurocranium. The formation of the unusually large basioccipital condyle for the vertebral column and the lack of the exoccipital condyle at the level of the temporal edge of the cranium are considered as distinguishing features of this species. The appearance of the bones of the ethmoidal region and certain bones of the splanchnocranium is also delayed. The projecting upper part of the cleithrum is considered a diagnostic feature of *P. antarcticum*. Four free pectoral radials develop from the radial cartilage, the upper subsequently fuses with the scapula. In early stages there are three pectoral interradial foramina between the radials which close from top to bottom except the lowest. The ossification of the axial skeleton has three centra: from urostyle posteriorly, from anterior part of notochord posteriorly and may also occur at the level of the third to fourth posterior ray of the second dorsal fin.

RÉSUMÉ. - Ce travail est une étude du dévelopment du squelette d'un poisson antarctique *Pleuragramma antarcticum* Boulenger (Nototheniidae). Par rapport au Nototheniidae déjà étudiés, le basioccipital et l'exoccipital se développent plus tard. La formation d'un très grand condyle articulaire du basioccipital pour l'articulation de la colonne vertébrale et le déplacement du condyle exoccipital au niveau de la marge temporal du crâne sont considérés comme des caractéristiques fondamentales de l'espèce *P. antarcticum*. L'apparition des os de la région éthmoïdienne et de quelques os du splanchnocrâne est également retardée. Le processus supérieur du cleithrum est considéré comme un indice diagnostique de *P. antarcticum*. Quatre radiaux libres se développent à partir du cartilage radial, le plus supérieur fusionnant avec la scapula. Dans les premiers stades on observe trois foramina interradiaux entre des radiaux et la scapula, qui se ferment ensuite sauf le plus inférieur. L'ossification du squelette axial a trois centra: l'urostyle, la région antérieure de la notochorde et (ce qui se rencontre plus rarement) le centre au niveau des troisième-quatrième rayons postérieurs de la deuxième nageoire dorsale.

Key-words. - Nototheniidae, *Pleuragramma antarcticum*, PS, Antarctic Ocean, Morphology, Ontogeny, Skeleton.

Among the primarily bottom dwelling notothenioid fishes of the Southern Ocean, only a few species have successfully occupied pelagic habitats. The Antarctic silverfish

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(1) Zoological Institute, Academy of Sciences (ZIN), St. Petersburg, RUSSIA.
(2) Murmansky Marine Biological Institute, Academy of Sciences (MMBI), Murmansk, RUSSIA.
(3) Alfred Wegener Institute, Bremerhaven, Germany (present address: National Park Office, Schlossgarten 1, D-25832 Tönning, GERMANY.

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Pleuragramma antarcticum Boulenger, 1902 is the only notothenioid fish with an entirely pelagic life history, although spawning may be demersal. The larvae ascend to surface waters after hatching, and the juvenile and adult fishes occur at increasing depths with age (Hubold, 1985). The morphological features of *P. antarcticum* characterize this species as the most specialized among secondarily pelagic notothenioids. Calcification of tissues is reduced leading to thin, easily lost scales, thin cranial bones and vertebrae which are not amphicoelous, but merely a thin collar of bone along with the conservation of the notochord (Eastman and DeVries, 1981; Voskoboinikova, 1982a, 1986; DeWitt *et al.*, 1990). Body weight is further reduced by the presence of subcutaneous lipid sacs (Eastman and DeVries, 1982). Typical features of a pelagic life-mode are the emarginate caudal fin, the interrupted cephalic canals of the seismo-sensorial system and presence of three lateral lines (Andriashev, 1965, 1987). The early development of external morphology features was described by Efremenko (1983), Keller (1983) and Kellermann (1990).

Until recently, data on the development of the bone skeleton of Antarctic fishes of the suborder Notothenioidei were fragmentary (Andriashev and Jakubovsky, 1971; Stevens *et al.*, 1984; Andriashev, 1987). The most comprehensive study was devoted to the development of the caudal fin skeleton of *Pleuragramma antarcticum* by Totton (1914). These data were complemented by studies of the osteological development of *Trematomus eulepidotus* Regan (Voskoboinikova and Tereshchuk, 1991) and the development of the pectoral girdle and caudal fin of *Nototheniops tchizh* (Shandikov, unpubl. data). Here, we attempt to describe the osteological development of *P. antarcticum* from the larval to the adult stage, and to compare it with the development of other nototheniids and of other perciform fishes. Growth in *P. antarcticum* is slow among notothenioids, so the question is: Is the osteological development retarded with respect to ontogenetical stages as can be anticipated from a secondarily, but truly pelagic species?

MATERIAL AND METHODS

The material used for our study belongs to the collection of larvae and juveniles of Antarctic fishes at the Alfred Wegener Institute for Polar and Marine Research (Germany). These were obtained from several German Antarctic expeditions to the Scotia Sea and the Antarctic Peninsula between 1975-87 (Kellermann, 1989). Some larvae and juveniles were available through the All-Union Scientific Research Institute of Fishery and Oceanography (Russia) and were politely given to us by the late V.N. Efremenko. Additional material was utilized from the Zoological Institute of the Russia Academy of Sciences from the D'Urville and Davis Seas.

A series of 40 larvae, juveniles and adults (from 17 to 169 mm SL) was studied using the methods of Hollister (1934) and Jakubowsky (1970). Since we do not have day-to-day series, we refer to the standard length to identify ontogenetic stages. Drawings were made with a drawing tube attached to a stereo microscope. For the skull and pectoral girdle we followed the terminology of Harrington (1955) and of Jollie (1986) which is currently used in osteological works, for the axial and caudal skeleton we adopted the terminology of Monod (1968). In the description of the osteological development we have followed Watson (1987).

RESULTS

Neurocranium (Fig. 1a-d)

Frontal. - The frontal, a rather well developed bone occurs at 30.0 mm SL as a long, thin plate on the roof of the skull, rounded at the posterior edge. At 44.0 mm, the bone is perforated by two small foramina (Fig. 1c), at 58.6 mm - by three foramina, at 72.6 mm - by four foramina for the rami of the superficial ophthalmic branch of trigeminal and facial nerves which disposed into a little groove along the lateral edge of the bone. At 83.1 mm, the anterior part of the groove forms a thin bony bridge between the second and third pores of the supraorbital canal of the seismo-sensory system; the posterior part of the groove is closed by the bony roof behind the third pore of the canal. Until 72.6 mm the frontals are separated by the cartilaginous endocranium medially and by the supraoccipital posteriorly. Beyond 72.6 mm the frontals close above the anterior part of the supraoccipital.

Parietal. - At 40.0 mm, a small rounded bone occurs behind the frontal, at 44.0 mm it overlaps with the posterior margin of the frontal and from 62.1 mm assumes a triangular shape.

Basioccipital, exoccipital, supraoccipital. - The basioccipital is a V-shaped bone plate closed in the middle part of the posterior end of the parasphenoid at 30 mm (Fig. 1b); behind it the cartilaginous endocranium forms a rather deep notch in which emerges the anterior end of the notochord. Thereafter, the bone quickly grows backwards as a broad triangular plate forming the condyle at the back tip at 40.0 mm. At 44.0 mm, the basioccipital has almost completely removed the notochord from the notch of the cartilaginous endocranium, the upper part of the condyle grows faster than the lower one, and at 58.6 mm it appears on the posterior side. At 62.1 mm, the condyle is fully formed and its size is unusually large in comparison with other species of nototheniids. In adult specimens the lower edge of the condyle curves downward.

The exoccipital occurs at 40.0 mm (Fig. 1c) as a small ossification lateral to the foramen magnum, more at the upper than at the temporal edge of the endocranium. At 44.0 mm this bone forms the well developed condyle for the first vertebrae and the lower part of the bone including the foramen for the vagus nerve. At 58.6 mm the upper part of the bone begins to develop, but meets its antimere in adults only. Later the condyle descends to the level of the temporal edge of the skull and its articular surface turns downward.

The supraoccipital first appears at 43.7 mm as a long ossification expanded at midregion. At 51.7 mm the bone forms a small posterior ridge, whereafter the supraoccipital broadens laterally at its midregion (62.1 mm). In adults this bone articulates the exoccipitals posteriorly.

Parasphenoid and pterosphenoid (= alisphenoid of ancient authors). - Larvae of 17.0 mm have the parasphenoid as a thin bone, pointed at the anterior end, which becomes longer and at 30.0 mm reaches the mid ethmoidal region of the skull, where the vomer closes it from below. At 40.0 mm the parasphenoid produces a small ascending process at both sides, which at 58.6 mm articulates with the prootic. In adults, the ascending process is broad and elongated, but do not reach the foramen for the trigeminal nerve and the pterosphenoid. The pterosphenoid appears at 51.7 mm as a narrow falcate-shaped bar underneath the frontal. Later it assumes a semicircular shape and begins to articulate with the prootic.

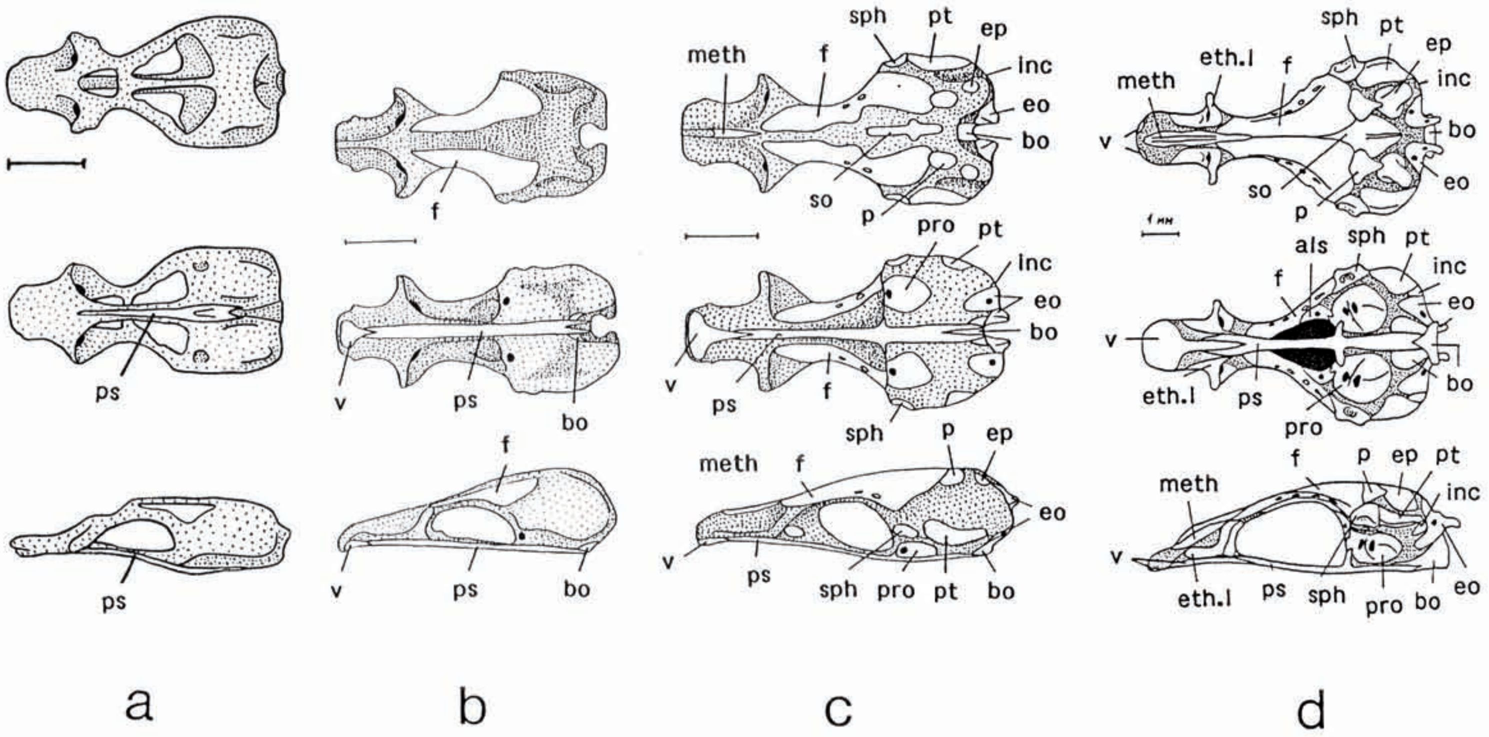

Fig. 1. - Development of the neurocranium in *Pleuragramma antarcticum*, showing dorsal (upper), ventral (middle) and left lateral (bottom) views. Standard lengths of specimens are: (a) 18.9 mm; (b) 33.0 mm; (c) 44.9 mm; (d) 76.2 mm. The scale bar is 1 mm. bo: basioccipital, eo: exoccipital, ep: epiotic, eth.l: lateral ethmoid, f: frontal, meth: mesethmoid, inc: intercalar, p: parietal, pro: prootic, ps: parasphenoid, pt: pterotic, ptsh: pterosphenoid, so: supraoccipital, sph: sphenotic, v: vomer. Cartilage stippled, ossifying white.

Vomer (Fig. 1b-d). - It first occurs in larvae of 30.0 mm as a thin triangular plate anteriorly below the surface of the ethmoidal cartilage. At 40.0 mm its anterior end broadens and at 44.0 m reaches the edges of the ethmoidal cartilage. At 58.6 mm the bone produces two slightly ascending processes, emerging at the dorsal surface of the ethmoidal cartilage. In adult fishes, the vomer is almost square shaped and has an elongate stem which reaches the level of the posterior edges of the lateral ethmoid.

Prootic, sphenotic, pterotic, epiotic (epioccipital), intercalar (opisthotic) (Fig. 1b-d). - The prootic is the first bone of the auditory region which appears at 40.0 mm as an oval ossification without foramina for the trigeminal and facial nerves. The first foramen appears at 58.6 mm, the second at 44.0 mm. In adults, the bone reaches below the parasphenoid, posteriorly - exoccipital and intercalar, upper to sphenotic, pterotic. At 43.7 mm there are small ossifications of all other bones of the auditory region. The sphenotic appears like a small roundish plate, which grows ventrally and forms two well developed processes along the temporal edge of the skull at 58.5 mm and a notch for the articular hyomandibular head on the lateral surface of the skull at 62.1 mm. Pterotic quickly grows anteriorly and reaches the sphenotic at 44.0 mm, and the frontal at 58.6 mm. In a larger specimen (58.6 mm) the broad lateral process of the pterotic was formed, the ventral surface of which is attached to the posterior articular process of the hyomandibular by ball-and-socket articulation. In adults the temporal canal of the seismo-sensory system is well developed and looks like a groove on the dorsal surface of the bone with a thin bony bridge above. The fully grown epiotic reaches the posterior edge of the vault of the skull and the frontal anteriorly at 58.6 mm. Later the epiotic curves laterally and forms the medial surface of the occipital cavity at 62.1 m. In adults the bone meets the supraoccipital medially, the exoccipital underneath, and the pterotic laterally. The intercalar appears as a little knob above the exoccipital at 58.6 mm, occupies the space between the latter and the pterotic (62.1 mm) and turns towards the upper surface of the vault of the skull in the occipital cavity region (72.1 mm). In adults the intercalar reaches the prootic on the lateral surface of the skull and articulates this bone above the bar of cartilage.

Mesethmoid and lateral ethmoid (Fig. 1c-d). - The mesethmoid first occurs at 40.0 mm as a rhomboidal plate anteriorly placed to the anterior end of the frontals. It quickly grows anteriorly and posteriorly and reaches the anterior margin of the frontals at 51.7 mm, then grows posteriorly between the frontals. At 72.1 mm the lateral surface of the bone touches the lateral ethmoid, and along the bone the longitudinal ridge is formed which later develops two small lateral plates anteriorly divided by a narrow notch. In adults the posterior process of the mesethmoid approaches the level of the posterior edge of the lateral ethmoid, the anterior lateral plates spread and touch laterally the margins of the ethmoidal region. The notch between these plates becomes deeper. The lateral ethmoid appears at 51.7 mm laterally to give the foramen for the olfactorial nerve. At 58.6 mm, a small horizontal part is formed in the anterior direction, the vertical part reaches full development. At 62.1 mm, the bone surrounds completely the foramen for the olfactorial nerve. In adults the anterior horizontal part of the bone is strongly developed, the vertical part turns posteriorly forming the upper arch of the eye orbit.

The nasal first occurs as an oval plate with a small hole in the center. At 58.6 mm the bone begins to curve slightly at both sides, at 72.1 mm the tube -like bone is formed.

Infraorbital bones. - The lacrimal appears at 30.0 mm as a long triangular plate with a hole near the posterior end. At 33.0 mm the bone broadens with a second hole appearing. The roof of the seismo-sensory canal begins to form at 72.1 mm, when all the pores are separated by thin bony bridges which are better developed in the posterior part of the bone. At 58.6 mm, the fourth infraorbital and dermosphenotic first appear as narrow triangular plates with a hole in the center. Both these bones acquire the tubular structure at 72.6 mm. The second and third infraorbitals do not occur in *P. antarcticum* and adults have an interruption in the infraorbital canal of the seismo-sensory system (Jakubowski, 1971; Andersen, 1984.

Splanchnocranium (Fig. 2-5)

Jaws. - All bones of the upper and lower jaws except the coronomeckelian are present in larvae of 17.0 mm and quickly assume their typical shape (Fig. 2a-d). The premaxilla at 18.9 mm has a small ascending process and larger articular and postmaxillar processes. At 43.7 mm in the base of the articular process there is a large foramen and the articular process joins to the bone with three thin bony bars only. At 72.6 mm the shape of

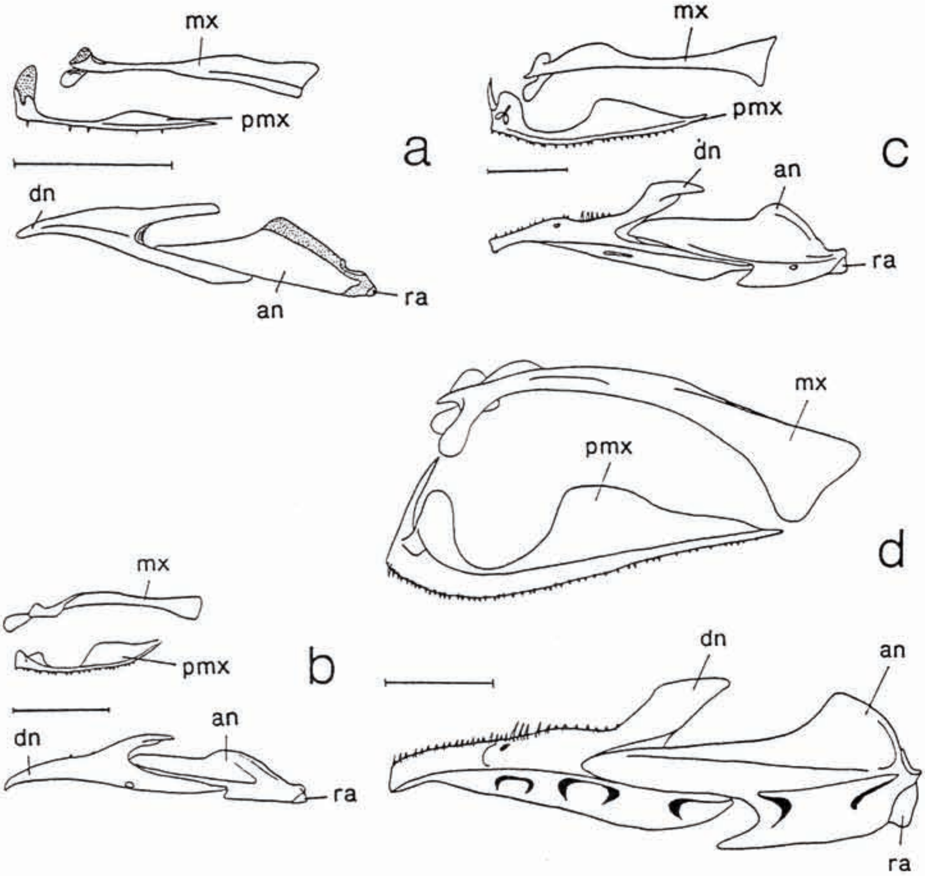

Fig. 2. - Development of the jaws in *Pleuragramma antarcticum*, left lateral views. Lengths of specimens in (a)-(d) as in figure 1. The scale bar is 1 mm. an: anguloarticular, dn: dentary, mx: maxilla, prmx: premaxilla, ra: retroarticular.

the premaxilla is identical with that of adults (Voskoboinikova, 1986). The maxilla at 17.0 mm has a well developed articular process, but the head of the bone is still incomplete and bordered by a broad cartilaginous bar. At 30.0 mm the maxilla has a well developed head. At 40.0 mm the small longitudinal ridge appears along the upper margin.

The dentary (Fig. 2a-d) has a tall and long coronoid process and a thin and long lower limb, which is slightly curved downward at the anterior end at 17.0 mm. The anterior end of Meckel's cartilage which has given the origin of the anterior part of the dentary as endochondral ossification then is included in the dermal parts of the dentary at all stages of ontogeny. Later the relative length of the coronoid process declines while its breadth increases and the coronoid process becomes more vertical. At 33.0 mm in the middle of the lower edge of the bone there is a small hole. At 44.0 mm it is closed by a small ridge which initiates the formation of the dentary seismo-sensory canal. At 58.6 mm anteriorly to this hole and also in the middle of the upper edge of the bone, numerous small holes appear, the upper of which transmit a branch of the lower jaw artery. The canal of the seismo-sensory system acquires some ridges along the lower edge of the bone and at 72.6 mm a roof forms between its pores.

Anguloarticular (articular of ancient authors) (Fig. 2a-d). - It appears as dermal and endochondral ossification of the posterior part of Meckel's cartilage. At 17.0 mm, the bone has a small anterior process which does not touch the base of the coronoid process of the dentary, there is no lower lobe of this bone. Posteriorly to the anguloarticular there is a large dorsal process of Meckel's cartilage. No seperate endochondral ossification which could be identified as articular of Nelson (1973) is found in the region of the facet of the quadrate. At 30.0 mm the dorsal process of Meckel's cartilage disappears, the anterior process of the anguloarticular becomes longer and touches the base of the coronoid process of the dentary. The lower lobe of the bone with a small hole for the seismo-sensory system nerve appears at 33.0 mm. At 44.0 mm two longitudinal ridges appear along the anterior process and the lower lobe of the bone forming the articular facet for the quadrate at the posterior ends. On the dorsal edge the coronoid process of the anguloarticular arises as epichondral element developed at 72.6 mm. Simultaneously along the anterior process the second longitudinal ridge forms and the canal of the seismo-sensory system acquires a roof.

Retroarticular (= angular of ancient authors) (Fig. 2a-d). - It occurs as endochondral ossification of the posterior end of the Meckel's cartilage at 17.0 mm. The bone gradually enlarges and assumes a triangular shape. At 40.0 mm it articulates with the anguloarticular, and after that the shape of the bone is square-like and posteriorly a small process for the attachment of the ligament of the interopercular is formed. The coronomeckelian first occurs as dermal ossification at 44.0 mm at the base of the anterior process of the anguloarticular and during development contains a roundish shape and small size. In adults, the posterior part of Meckel's cartilage lies as a longitudinal thin bar along the medial surface of the anguloarticular.

Jaw teeth (Fig. 2a-d). - The first are observed on the premaxilla at 18.9 mm. Some villiform teeth are in the connective tissue separately from the ventral surface of the premaxilla, the largest tooth is at the symphysis of the premaxilla. At 30.0 mm the number of teeth increases, they attach to the premaxilla in a single row. There are two small teeth in the middle of the upper edge of the dentary. Later the number of jaw teeth gradually increases and they are arranged in two irregular rows at 62.1 mm. Size differentiation of teeth is completed at 62.1 mm. Two strong, sharp, conical teeth are at the symphysis of the premaxilla and three such teeth in the middle of each dentary. The same arrangement of teeth is noted by several authors in adults (Norman, 1938; Voskoboinikova, 1982a; DeWitt *et al.*, 1990).

Quadrate, palatine (= autopalatine of some authors), ecto-, meso- and metapterygoids (Fig. 3a-d). - The process of the quadrate first occurs at 18.9 mm as a thin dermal bone disposed on the lateral surface of the ventral end of the hyosymplectic cartilage (Fig. 3a) and can be considered as quadratojugal. Later at 30.0 mm, the chondral element of the quadrate appears in the ventral posterior part of the palatoquadrate cartilage, grows anteriorly and at 40.0 mm has a well developed head for the joint with the articular. Posteriorly, the dermal element fuses with the chondral part of the quadrate forming the posterior process of this bone. Later the upper edge of the bone grows and touches the lower edge of the ectopterygoid, lying on it from above (62.1 mm). The height of the posteroventral process increases and posteriorly the process touches the vertical limb of the preopercle, and acquires the usual shape found in adults. The palatine first occurs at 40.0 mm as a thin narrow bar at the upper end of the palatoquadrate cartilage, then its head and stem are formed and at 62.1 mm the bone reaches the upper end of the ectopterygoid, at 72.6 mm the mesopterygoid posteriorly. The mesopterygoid occurs at 30.0 mm along the dorso-medial edge of the palatoquadrate cartilage as a thin narrow bar which spreads dorsally and posteriorly touches the metapterygoid. The metapterygoid ossifies at 30.0 mm at the posterior end of the palatoquadrate cartilage. Then its anterior end quickly grows ventrally reaching the symplectic at 40.0 mm, anteriorly the mesopterygoid and the quadrate in adults. At 58.6 mm the bone has a fairly well developed posterior limb lying on the hyomandibular. The ectopterygoid first occurs as a narrow bar along the anterior edge of the palatoquadrate cartilage. Then it acquires a falcate shape.

Symplectic and hyomandibular (Fig. 3). - The first appearance of the symplectic occurs at 30.0 mm in the lower part of the hyosymplectic cartilage of the hyoid arch. At 40.0 mm it reaches the quadrate and then joins the facet at the inner surface of the quadrate. The posterior end of the symplectic forms the articulation with the hyomandibular across the cartilaginous bar at 72.6 mm. The hyomandibular is first found at 30.0 mm as an oval ossification at the anterior edge of the hyosymplectic cartilage including the foramen for the facial nerve. At 58.0 mm the bone reaches the upper and posterior edges of the cartilage and the articular processes are formed which acquire the adult shape at 72.6 mm.

Cerato- (anterior ceratohyal of some authors), epi- (posterior ceratohyal of some authors), hypo-, inter-, basi- and urohyals, branchiostegal rays (Fig. 4a-d). - The first ossification in the hyoid cartilage is the ceratohyal at 17.0-18.9 mm which at 30.0 mm represents about 2/3 of the lower part of the hyoid arch. At 72.6 mm it meets the upper and lower hypohyals anteriorly and the epihyal posteriorly across the cartilage bar. Complete cerato- and epihyals occur in adults. Epihyal is observed at 30.0 mm as a small roundish ossification at the posterior end of the lower part of the hyoid arch. Then it grows and reaches the posterior margin of the cartilaginous hyoid arch. After that, it acquires the typical adult triangular shape at 72.6 mm. The lower hypohyal is seen in larvae of 30.0 mm as a small knob anterior and ventral to the ceratohyal. At 40.0 mm it acquires the shape of a cup on the lower anterior end of the cartilaginous hyoid arch, posteriorly a small process is formed. The upper hypohyal is found on the dorsal surface of the anterior end of the hyoid arch at 51.7 mm as a small bony plate which later enlarges and turns on the medial surface of the hyoid cartilage. At 72.6 mm it reaches the ceratohyal posteriorly. The articulations

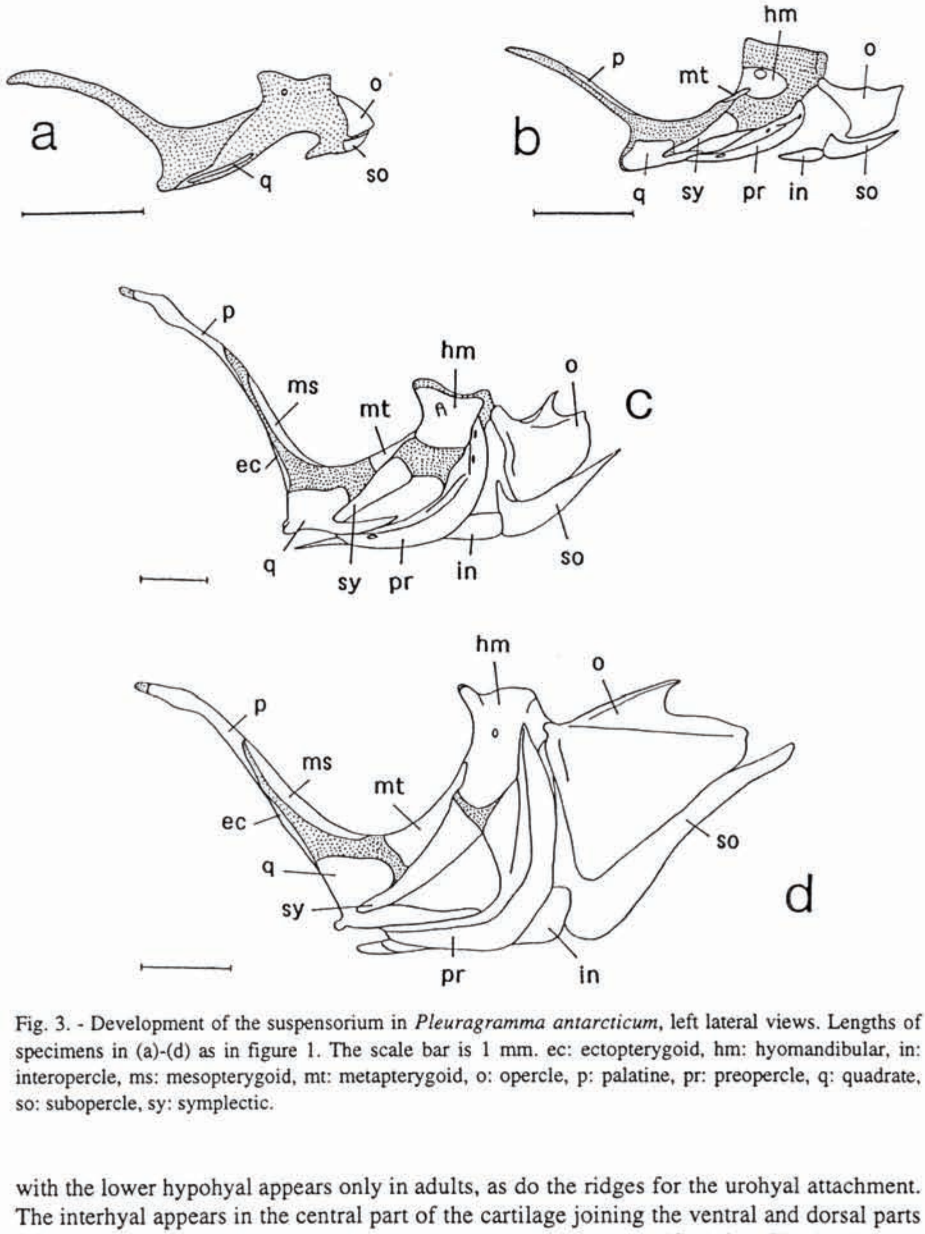

Fig. 3. - Development of the suspensorium in *Pleuragramma antarcticum*, left lateral views. Lengths of specimens in (a)-(d) as in figure 1. The scale bar is 1 mm. ec: ectopterygoid, hm: hyomandibular, in: interopercle, ms: mesopterygoid, mt: metapterygoid, o: opercle, p: palatine, pr: preopercle, q: quadrate, so: subopercle, sy: symplectic.

with the lower hypohyal appears only in adults, as do the ridges for the urohyal attachment. The interhyal appears in the central part of the cartilage joining the ventral and dorsal parts of the hyoid arch at 44.0 mm and until the adult stage has unossified tips. The basihyal is observed near the posterior end of its cartilage plate at 44.0 mm as a small horseshoe-like ossification which later grows anteriorly and posteriorly and acquires the typical triangular shape. The cartilaginous plate at the anterior edge of the basihyal is conserved in adults. The urohyal appears at 33.0 mm as a small bony stick. Then it enlarges and along its

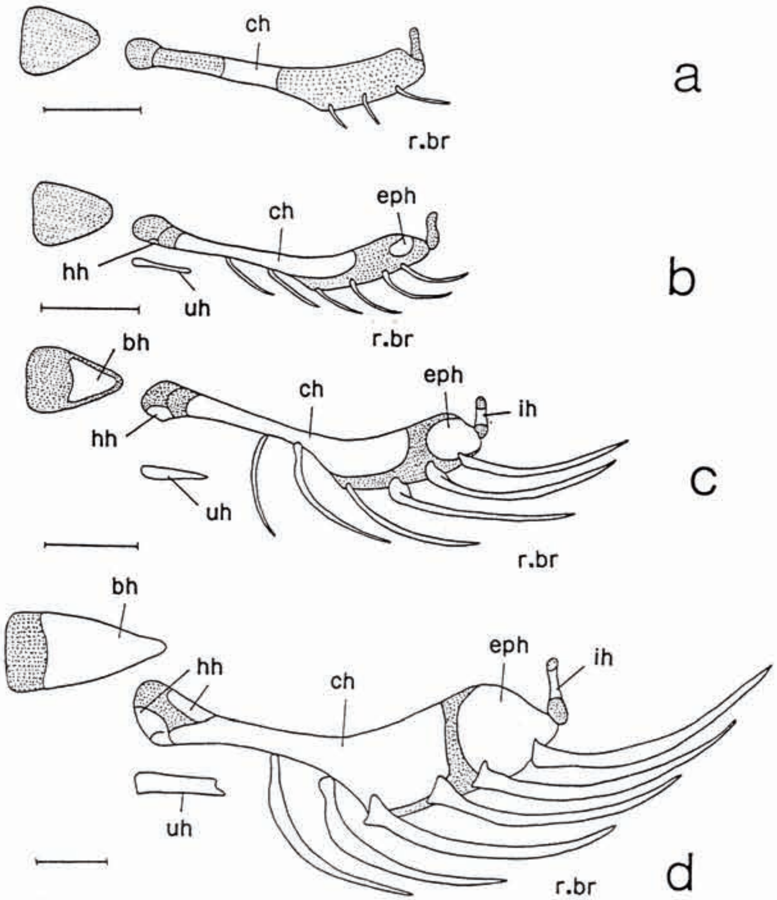

Fig. 4. - Development of the ventral part of the hyoid arch in *Pleuragramma antarcticum*, left lateral views. Lengths of specimens in (a)-(d) as in figure 1. The scale bar is 1 mm. bh: basihyal, ch: ceratohyal, eph: epihyal, hh: hypohyals, ih: interhyal, r.br: branchiostegal rays, uh: urohyal.

ventral margin the lateral projections are formed. In larvae of 18.9 mm three branchiostegal rays are noted, at 30.0 mm there are six branchiostegal rays. Their relative length and breadth gradually increase and at 72.6 mm their length represents about half the lenght of the lower part of the hyoid arch, like in adults. At 83.1 mm four posterior branchiostegal rays show the small sharpened anterior processes on their tips, in adults these are also on two anterior rays.

Opercle, preopercle, subopercle, interopercle (Fig. 3a-d). - Among the bones of the opercular series opercle, the sub- and preopercle first are found at 17-19 mm. A well developed interopercle is present at 30.0 mm. The opercle first is a triangular plate, at 33.0 mm it forms a small dorsal process and anteriorly the head to join the hyomandibular.

At 40.0 mm the upper process is well developed and sharpened and the posterior end of the opercle becomes longer, like in adults.

The preopercle first appears as a thin ossification along the lower edge of the hyoid cartilage. At 40.0 mm its vertical and horizontal branches are clearly seen and at 51.7 mm they become longer and curve towards each other. At 72.6 mm, the bone forms the small flat plate between its branches. There are two holes of the canal of the seismo-sensory system. The subopercle, as a long triangular plate with a small articular process lies along the lower edge of the opercle. At 72.6 mm the height of the vertical branch increases and represents about 2/3 of the length of the anterior edge of the opercle. The posterior end of the bone grows and at 58.6 mm comes out of the posterior end of the opercle. The interopercle, first a thin triangular plate attaching to the subopercle at 30.0 mm, broadens at its posterior end and remains thread-like in the anterior part until 62.1 mm. At 72.1 mm, the broad anterior end reaches the level of the articular condyle of the quadrate.

Basi-, hypo-, cerato-, epi- and pharyngobranchials (Fig. 5a-c). - The first bony elements which appear in the gill arch skeleton are the ceratobranchials stained at 17.0 mm and also a few teeth on the pharyngo- and ceratobranchials 5. At 30.0 mm there is ossification of the pharyngobranchials, the latest of which (Phbr. 5) is very small. Later, few gill rakers begin to ossify on ceratobranchials 1 - 4 at their dorsal ends. Gill rakers in the first row are elongated and without denticles but in all other rows gill rakers have numerous denticles. At 40.0 mm there are ossified hypobranchial 1, basibranchial 3, and epibranchial 1, 3, 4; at 44.0 mm - hypobranchial 2, epibranchial 2, basibranchial 1. Ossification of hypobranchyal 3 (51.7 mm) and basibranchial 2 (83.1 mm) occurs later. All bones of the gill arches are characterized by an elongated and thinned shape which is found in adults. The size of teeth quickly enlarges and teeth become sharp-conical. At 40.0 mm gill rakers begin to develop on the hypo- and epibranchials. Rakers of the first row are attached to the bones by elongated processes. Other rakers are not attached until the adult stage. The epibranchials, first as thin sticks begin to curve outward at 51.7 mm and form the little processes that are better developed in the third and fourth epibranchials. Later the breadth of the bones and the size of the processes enlarge and at 83.1 mm the processes of epibranchials 3 and 4 articulate each other.

Pectoral girdle (Fig. 6a-c)

The cleithrum is found as a thin sharp stick at 17.0 mm. Later, it broadens along its whole length, and a thorn-like process forms at the upper end at 40.0 mm. Posterior to the process, the upper lobe of the cleithrum arises, separated from the process by a forked depression. In the lower part of the cleithrum a small longitudinal ridge appears. The upper lobe of the cleithrum grows dorsally reaching the level of the tip of the thorn-like process at 62.1 mm. In adult and juvenile *P. antarcticum* most of the bone (about 1/3 - 1/4) protrudes above the scapula and the base of the process is higher than the level of the scapula also in comparison with other species of nototheniids. The longitudinal ridge of the cleithrum is fully formed at 58.6 mm. At 30.0 mm a small curved post-temporal and the supracleithrum appear as thin bony plates. Their formation is completed at 58.6 mm when the post-temporal acquires two well developed processes and the supracleithrum has the articular head at the upper end. At 44.0 mm in the radial cartilage four small bony radials occur. At 44.0 mm, they become longer and three interradial wholes appear along the dorsoposterior edge of the radial cartilage between the radials. The fourth interradial hole lies between the scapula and the upper radial which fuse at 62.1 mm. At 83.1 mm there are all four

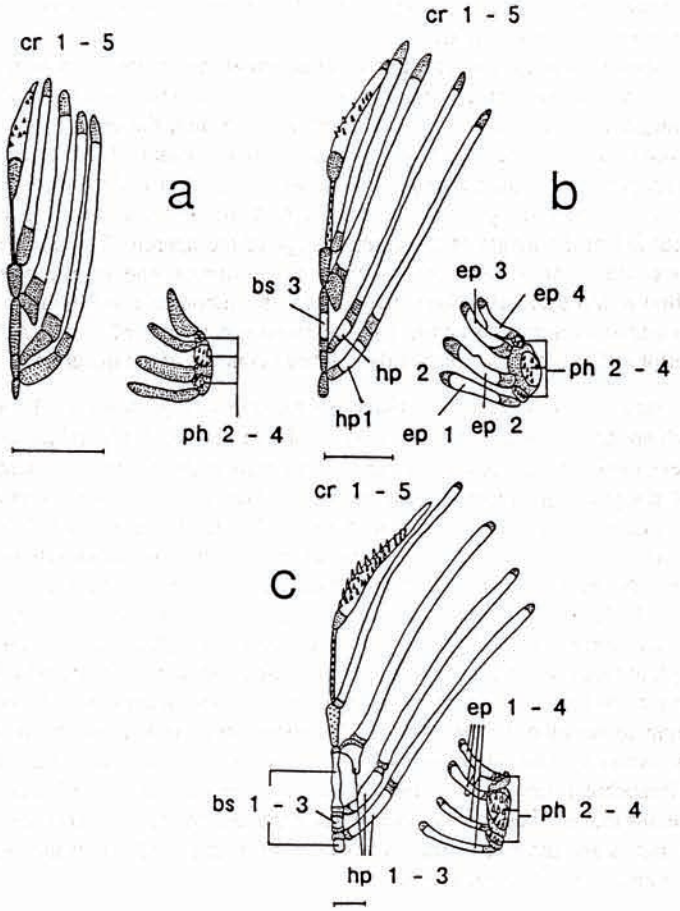

Fig. 5. - Development of the branchial skeleton of *Pleuragramma antarcticum*, dorsal lateral views for ventral parts of arches, ventral views for dorsal parts of arches. Lengths of specimens shown in (a)-(c) are 30.0 mm, 44.0 mm, 83.1 mm SL. The scale bar is 1 mm. bs: basibranchial, cr: ceratobranchial, ep: epibranchial, hp: hypobranchial, ph: pharyngobranchial.

plus a small hole near the anterior edge of radial 4. In adults there is only one interradial hole between the lowest radials, if any. The scapula first appears at 44.0 mm as a triangular bone behind the scapular foramen in the cartilage plate of the primary pectoral girdle. It grows rapidly anteriorly and around the scapular foramen from below, enclosing it at 62.1 mm. The coracoid appears at 44.0 mm also in the lower part of the cartilage plate of the primary pectoral girdle. Then it quickly spreads completing its development at 62.1 mm. At this size the coracoid has well developed anterior and postcoracoidal processes, at the base of the latter there is a small postcoracoidal foramen. In adults the coracoid articulates with the lowermost radial across the cartilage bar.

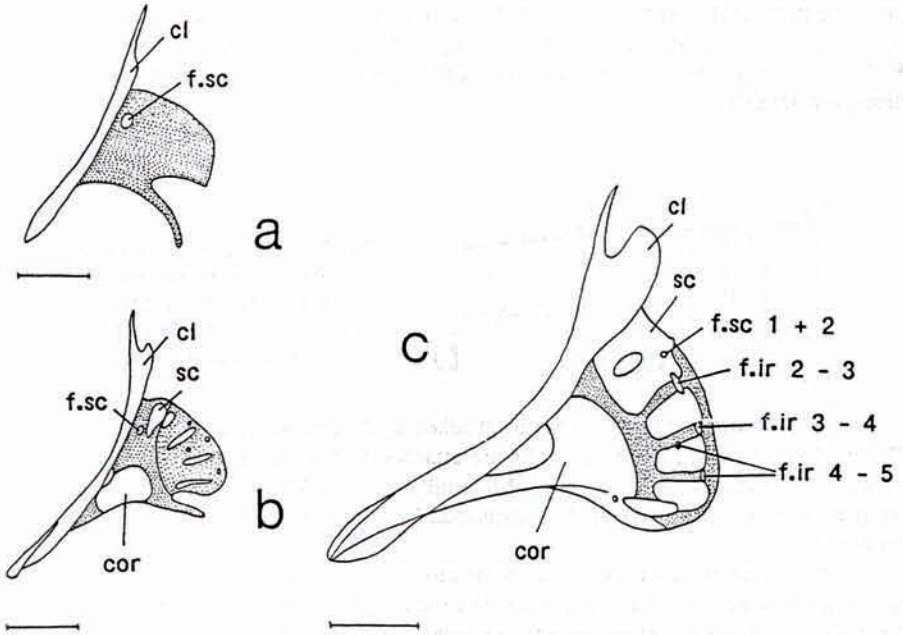

Fig. 6. - Development of the pectoral girdle and pectoral radials in *Pleuragramma antarcticum*, left lateral views. Lengths of specimens shown in (a)-(c) are: 33.0 mm, 44,0 mm, 76.2 mm SL. The scale bar is 1 mm. cl: cleithrum, cor: coracoid, f.ir: interradial foramen, r: radial, sc: scapula, f.sc.: scapular foramen.

At 17.0 mm larvae have 16-18 pectoral rays, at 19.0-20.0 mm there are 19-22 rays which corresponds to the number in adults.

Axial skeleton

The appearance of the vertebral column begins from the urostyle at 17.0 mm. Ossification proceeds to the hypurals, from hypural 1-2 to hypurals 3 and 4, to the parhypural and then in the haemal and neural arches of the pleural vertebrae. A second center of ossification lies behind the basioccipital. Here the ossification of the neural and haemal arches is observed at 40.0 mm and 47.0 mm correspondingly. Full development of the neural and haemal arches with well developed neural and haemal spines of all vertebrae is observed at 89.0 mm. In adults the neural and haemal arches are poorly developed and have short spines also noted by other authors (Norman, 1938; Balushkin, 1984). The vertebral centrum 1 appears at 43.7 mm as two small oval ossifications on the sides of the notochord. It is a typical autocentrum which is formed without participation of the fibrous part of the chordal sheath and arcualia (François, 1967; Schultze and Arratia, 1989). Larger specimens of 44.0-49.0 mm have a few centra in the anterior part of the notochord and also at the level of the posterior rays of the second dorsal fin. The bony plates lie usually two by two lateral to the notochord dorsally and ventrally and join medially. Then the plates of both sides join dorsally and ventrally and form the bony ring around the notochord (Fig. 7), meeting the arcualia. The formation of most vertebral centra is completed at 51.7 mm.

Only the trunk centra do not join ventrally until 62.1 mm. In the last five or six vertebrae the saddle-shaped ossifications occur dorsally and ventrally which then join laterally at 89.9 mm. Zygapophyses begin to develop at 83.1 mm from the basioccipital and from the urostyle anteriorly.

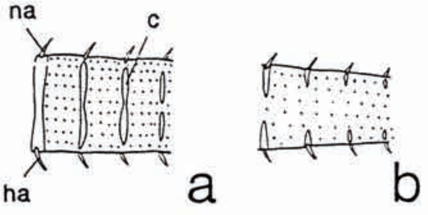

Fig. 7. - Schematic development of the vertebral centra in the middle (a) and posterior (b) parts of the vertebral column. Length of specimen is 48.6 mm. c: centrum, ha: haemal arch, na: neural arch.

At 51.7 mm eight epipleural ribs attached to the first to eighth vertebrae are found. On the 4-9th vertebrae six pleural ribs are attached to the parapophyses. The number of pleural ribs gradually increases to 9-12 in adults, the last 3-4 ribs are not attached to the parapophyses and lie freely in the myosepta. The number of epipleural ribs in adults reaches 10.

The onset of the development of the proximal interhaemals was noted at 40.0 mm, of the interneurals at 43.7 mm at the level of the middle of the second dorsal and anal fins from where ossification gradually spreads anteriorly and posteriorly. Full development of proximal pterygiophores ends at 62.1 mm, with the interneurals of the first dorsal fin being the latest to ossify. In adult *P. antarcticum* special articular surfaces for the distal pterygiophores are found on the dorsal surface of the anterior pterygiophores. The distal pterygiophores remain cartilaginous, only in adults small lateral ossifications appear.

Caudal fin skeleton (Fig. 8a-d)

As noted above, the urostyle is the first ossification of the axial skeleton, and at 17.0 mm it is an unpair thin bone on the dorsal part of the notochord. Later it grows ventrally and acquires a conic shape with an oval foramen below. This foramen remains until 51.7 mm. The urostyle appears and exists as the only center, so it remains impossible to assess how many centra serve as predecessors of this compound structure in nototheniids. One specimen of *P. antarcticum* of 47.0 mm had a double urostyle with two cones in sequence. At 17.0 mm the following cartilaginous elements are noted: three hypurals (two in the epaxial lobe) and the parhypural. At 19.0 mm in the cartilage three hypuralia corresponding to the bone hypuralia are noted. At 30.0 mm both epaxial and hypaxial lobes have one hypural with an unossified distal portion. The parhypural is almost completely ossified. Bony epurals were found first at 76.2 mm. In adults the epaxial hypural fuses with the urostyle. The uroneural is not existent in *P. antarcticum* (Totton, 1914; Andersen, 1984; Balushkin, 1984, 1989). This bone is also lacking in our specimens. However, in a juvenile 89.9 mm two very small bones are found between the ventral edge of the epural and dorsal surface of the urostyle, so they may be considered as the remainders of two uroneurals.

The number of epurals in *P. antarcticum* is variable (Fig. 8a-d). There are specimens with one, two or three epurals. The formation of one or two epurals seems to be the result of fusion of cartilaginous and bony element traces which are seen in specimens of 89.0 and 132.5 mm.

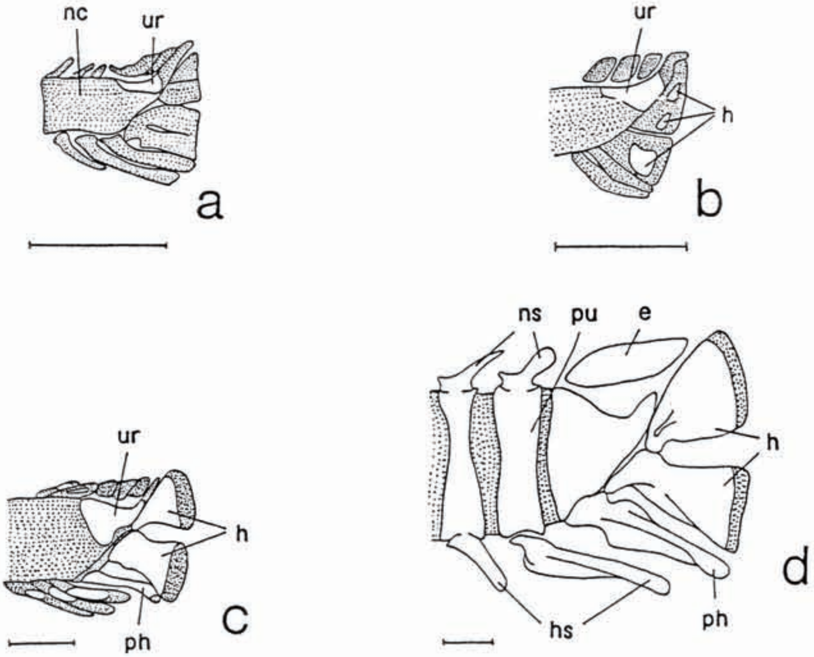

Fig. 8. - Development of the hypural complex in *Pleuragramma antarcticum*, left lateral views. Lengths of specimens in (a)-(d) as in figure 1. The scale bar is 1 mm. e: epural, hs: haemal spine, h: hypural, nc: notochord, n: neural spine, ph: parhypural, pu: pleural centrum, ur: urostyle.

Fin rays

Pectoral and caudal fins have the most rapid appearance among the fins. At 17.0 mm in the pectoral fin there are 16-18 rays, in the caudal fin there are 15-16 principal rays and two upper and one lower procurrent rays. The number of unbranched rays increases until 50.0 mm when about 11-12 rays are present above and below. At 17.0-19.0 mm the onset of ray ossification in the middle of the second dorsal fin and the anal fin is observed after which it spreads anteriorly and posteriorly and ends at 30.0 mm. The appearance of the rays in the first dorsal fin begins at 35.0 mm (Keller, 1983; Kellermann, 1990) and ends at 40.0 mm. The final pelvic fin rays appear at 40.0 mm.

DISCUSSION

The most conspicuous differences both in the succession of appearance and in the morphogenesis of bones between *Pleuragramma antarcticum* and other nototheniid species (e.g., *Trematomus eulepidotus*) are found in the occipital region of the neurocranium (Table I). Late ossification of the basi- and exoccipital as compared with the parasphenoid of *P. antarcticum* was not found in *T. eulepidotus* (Voskoboinikova and Tereshchuk, 1991) where these three bones appear almost simultaneously. In *P. antarcticum* a rather deep notch in the posterior end of the cartilaginous vault of the skull exists for some time and

Table I. - Sequence of appearance of different bones during the ontogeny of *Pleuragramma antarcticum*.

Bones SL mm	17.0	18.9	30.0	33.0	40.0	43.7	46.0	51.7	58.6
mesethmoid	-	-	-	-	+	+	+	+	+
lateral ethmoid	-	-	-	-	-	-	-	+	+
frontal	-	-	+	+	+	+	+	+	+
nasal	-	-	-	+	+	+	+	+	+
parietal	-	-	-	-	+	+	+	+	+
vomer	-	-	+	+	+	+	+	+	+
parasphenoid	+	+	+	+	+	+	+	+	+
pterosphenoid	-	-	-	-	-	-	-	+	+
prootic	-	-	-	-	+	+	+	+	+
sphenotic	-	-	-	-	-	+	+	+	+
pterotic	-	-	-	-	-	+	+	+	+
epiotic	-	-	-	-	-	+	+	+	+
intercalar	-	-	-	-	-	-	-	-	+
posttemporal	-	-	+	+	+	+	+	+	+
supraoccipital	-	-	-	-	-	+	+	+	+
exoccipital	-	-	-	-	+	+	+	+	+
basioccipital	-	-	+	+	+	+	+	+	+
maxillae	+	+	+	+	+	+	+	+	+
premaxillae	+	+	+	+	+	+	+	+	+
dentary	+	+	+	+	+	+	+	+	+
anguloarticular	+	+	+	+	+	+	+	+	+
retroarticular	+	+	+	+	+	+	+	+	+
palatine	-	-	-	-	+	+	+	+	+
quadrate	+	+	+	+	+	+	+	+	+
ectopterygoid	-	-	-	-	+	+	+	+	+
mesopterygoid	-	-	+	+	+	+	+	+	+
metapterygoid	-	-	+	+	+	+	+	+	+
hyomandibular	-	-	+	+	+	+	+	+	+
symplectic	-	-	+	+	+	+	+	+	+
interhyal	-	-	-	-	-	+	+	+	+
epihyal	-	-	+	+	+	+	+	+	+
ceratohyal	+	+	+	+	+	+	+	+	+
upper hypohyal	-	-	-	-	-	-	-	+	+
lower hypohyal	-	-	+	+	+	+	+	+	+
basihyal	-	-	-	-	-	+	+	+	+
urohyal	-	-	-	+	+	+	+	+	+
basibranchial 1	-	-	-	-	-	+	+	+	+
basibranchial 2	-	-	-	-	-	-	-	-	83.1
basibranchial 3	-	-	-	-	+	+	+	+	+
hypobranchial 1	-	-	-	-	+	+	+	+	+
hypobranchial 2	-	-	-	-	-	+	+	+	+
hypobranchial 3	-	-	-	-	-	-	-	+	+
ceratobranchials 1 - 4	+	+	+	+	+	+	+	+	+
epibranchial 1	-	-	-	-	+	+	+	+	+
epibranchial 2	-	-	-	-	-	+	+	+	+
epibranchial 3	-	-	-	-	+	+	+	+	+
epibranchial	-	-	-	-	+	+	+	+	+
pharyngobranchials 2 - 4	-	-	+	+	+	+	+	+	+
opercle	+	+	+	+	+	+	+	+	+
preopercle	-	-	+	+	+	+	+	+	+
interopercle	-	-	+	+	+	+	+	+	+
subopercle	-	+	+	+	+	+	+	+	+
lacrimal	-	-	+	+	+	+	+	+	+
infraorbital 4	-	-	-	-	-	-	-	-	+
dermosphenotic	-	-	-	-	-	-	-	-	+
cleithrum	+	+	+	+	+	+	+	+	+
coracoid	-	-	-	-	-	+	+	+	+
scapula	-	-	-	-	-	+	+	+	+
radials 2 - 5	-	-	-	-	+	+	+	+	+
supracleithrum	-	-	+	+	+	+	+	+	+
urostyle	+	+	+	+	+	+	+	+	+
hypurals 1 - 2, 3,4	-	-	+	+	+	+	+	+	+
epurals	-	-	-	-	-	-	-	-	76.7

later is filled by the basioccipital. Moreover, the basioccipital condyle is unusually large which may be related to the large size of vertebrae and to the life-long persistence of the notochord in *P. antarcticum* (Eastman and DeVries, 1981, 1982). The development of the occipital bones differs markedly from the development observed in *T. eulepidotus* in which the occipital condyle is smaller and the exoccipital condyle lies beside the basioccipital condyle. No similar development is found in the literature of perciformes (Mook, 1977; Fritzsche and Johnson, 1980; Watson, 1982, 1987; Karrer, 1984; Matsuoka, 1985; Lindemann, 1986). Thus, we assume that the unique development of the occipital bones is an autapomorph feature of *P. antarcticum*. Another difference between *P. antarcticum* and *T. eulepidotus* is the late ossification of the supraoccipital in the latter species. It is known that all the fishes of the subfamily Trematominae have the rather weak ossification of the occipital region (Balushkin, 1982) which can be related to the late ossification of the supraoccipital and the upper parts of the exoccipitals.

The development of the splanchnocranium of *P. antarcticum* is close to the development in *T. eulepidotus*. They are characterized by the earliest appearance of the jaw bones (except the coronomeckelian); the latest appearance of the interopercle in the opercle series, ectopterygoids in the palatoquadrate arch, the upper hypohyal in the lower part of the hyoid arch, hypobranchial 3 and basibranchial 2 in the gill arches. In both species the articulation of the meso- and metapterygoid occurs only in adults. Iwami (1985) finds a weak development or a loss of the upper hypohyal in the most specialized species of the notothenioid family Channichthyidae (according to the scheme of Regan, 1913), and the other specialized family Bathydraconidae the loss of the upper hypohyal is noted in the most specialized species (Voskoboinikova, unpubl. data). The basibranchial 2 is lost in the families Harpagiferidae, Artedidraconidae, Bathydraconidae, Channichthyidae (Iwami, 1985). The loss of the articulation of the meso- and metapterygoids is also noted in the specialized notothenioid families Artedidraconidae (Eakin, 1981), Bathydraconidae and Channichthyidae (Norman, 1938), and in the nototheniid *Aethotaxis mitopteryx* (Voskoboinikova, 1986). We consider all these cases of reduction of the bony elements which appear late during ontogeny as an illustration of the Mehnert (in Severztov, 1939) and Severtzov (1939) rule that the elements which appear later during ontogeny usually disappear in the more specialized taxa as a result of a reduction. Balushkin (1978) notes that these elements show the large variability of the structure.

In the splanchnocranium of *P. antarcticum* the complicate nature of the quadrate is found. First the dermal bone occurs at the ventroanterior edge of the hyosymplectic cartilage, then the chondral quadrate ossifies in the ventral part of the palatoquadrate cartilage, followed by the fusion of both bones and the formation of the posterior process of the quadrate by the dermal element. We consider the dermal element of the quadrate as the homologue of the quadratojugal of lower osteichthyans following the view of some authors (e.g., Jollie, 1986). Arratia and Schultze (1991) observe the formation of the posterior process of the quadrate in some teleost species from the connective tissue and noted that the perichondral ossification of the quadrate always precedes the appearance of the membranous posterior process. Therefore, these authors assume that there is no appearance of the quadratojugal in the ontogeny of teleosts. However, in *P. antarcticum* the dermal element of the quadratum appears first and moreover it relates to the hyosymplectic and not to the palatoquadrate cartilage so it seems possible that it is the quadratojugal.

In *P. antarcticum* and in *T. eulepidotus* the same succession in the appearance and development of bony elements of the pectoral girdle and fin is found. This type of development is also observed by Andriashev (1987) for the notothenioid *Bovichtus* *variegatus* and by Shandikov for *Nototheniops tchizh* (pers. comm.). An important difference between notothenioids and other perciform fishes is the fusion of the upper two radials with the scapula, and the resulting persistance of only three free radials in adults is the diagnostic feature of the suborder Notothenioidei (Regan, 1913). Some authors (Gregory, 1933; Balushkin, 1984, 1989) note the complex nature of the scapula in notothenioids formed by fusion of the two upper radials with the scapula. This is confirmed by the existence of interradial holes in the scapula and between scapula and the upper radials. The result of our study supports the hypothesis that fusion has occurred between the uppermost radials with the scapula during the phylogeny of notothenioids.

Balushkin (1984) pays great attention to the number of interradial holes to evaluate the degree of specialization of the pectoral girdle: their number decreases in the more specialized species. The ontogenetic development of this feature in *P. antarcticum* is corresponding to the closing of the interradial holes in phylogeny of nototheniids (Balushkin, 1984, 1989), so in adults only the lowermost hole remains or may be absent.

For the classification of nototheniids the position of the scapular foramen is very important. It may lie in the scapula or between scapula and coracoid (Boulenger, 1902; Regan, 1913; Balushkin, 1984, 1989). In *P. antarcticum* the foramen is in the scapula. Another special feature of *P. antarcticum* is the rather long upper limb of the cleithrum with a spine-like process, the base of which is higher than the upper edge of the scapula in contrast to all other nototheniids. Thus, we consider this feature as autapomorphy for *P. antarcticum*.

Potthoff *et al.* (1988), basing on a comparative analysis of their own and literature data on the development of the axial skeleton in certain teleosts propose several types of sequence of appearance of the different elements. In a comparison with other perciforms *P. antarcticum* is characterized by its own type of appearance of the bony elements of the axial skeleton with the presence of three centra of ossification at the urostyle, the anterior end of the notochord and at the level of the 3-4 last rays of the second dorsal fin, and with the primary appearance of the posterior neural and haemal arches. The development of autocentra begins at the lateral sides of the notochord as in several perciforms (Potthoff *et al.*, 1988). During ontogeny *P. antarcticum* conserves the very specialized structure of vertebrae in that there is no central part of the centra and the notochord passes through the vertebral column (Totton, 1914; Eastman and DeVries, 1981; DeWitt *et al.*, 1990).

The sequence of appearance and development of the pleural and epipleural ribs correspond to the sequence described for some percoids by Potthoff *et al.* (1988) and for blennioids by Watson (1987), but their number increases to 12 for the pleural ribs and to 10 for the epipleural ribs in *P. antarcticum*.

Stevens *et al.* (1984) reported the following succession for the appearance of fin rays in nototheniids: pectoral, caudal, pelvic, dorsal and anal fins. Our results confirm the succession reported by Keller (1983) for *P. antarcticum* and Kellermann (1990) for nototheniids: pectoral, caudal, second dorsal, anal, first dorsal and pelvic fins.

A detailed study of the development of the caudal skeleton of *P. antarcticum* from 8 mm notochord length onward was performed by Totton (1914). He followed the changes in the structure of cartilaginous elements and characterized some stages of the skeletal development. Our data confirm the view of Totton (1914) that the origin of the axial skeleton development is at the posterior end of the notochord. The succession of the appearance of bones corresponds to the succession of the cartilaginous skeleton noted by Totton (1914). The same succession is noted for *T. eulepidotus* (Voskoboinikova and

Tereshchuk, 1991). Totton (1914) notes two neural and two haemal arches on the pleural centrum 1 in his specimens of *P. antarcticum* and other nototheniids. In our material we found specimens with and without two neural and two haemal arches. Further, some variability is observed in the number of epurals - from one to three. Possibly a reduction of the epural number is a result of fusion of these elements, traces of which were found in two of our specimens. Balushkin (1984, 1989) notes the existence of an additional element in some nototheniid specimens which he considers as first epural. In his opinion this additional element may participate in the formation of two neural arches of the pleural centrum. Basing on the absence of the shortened neural arch at the pleural centrum, Balushkin (1984, 1989) proposes that in nototheniids the pleural centrum 2 is a part of the compound urostyle and its neural arch can appear as additional epural. In *P. antarcticum* only one ural centrum develops during ontogeny and there are no traces of more ural centra which in our opinion does not deny the existence of a compound urostyle in ancestors of this very specialized species.

Three hypurals appear in the early stages of *P. antarcticum* of which the two epaxial hypurals fuse at 30.0 mm SL and later fuse with the urostyle. During development of *T. eulepidotus* the fusion of bony hypurals is also observed first in the hypaxial and later in the epaxial lobes (Voskoboinikova and Tereshchuk, 1991). Such a fusion is also found in *Nototheniops tchizh* (Shandikov, pers. comm). The succession of hypural fusion in the ontogeny of nototheniids corresponds to the succession in the phylogeny of this group described by Balushkin (1984, 1989). The process of hypural fusion during ontogeny is a widely spread phenomenon among teleosts (e.g., Berry, 1969; Potthoff, 1975; Mook, 1977; Potthoff *et al.*, 1988).

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